

Red Algae Respond to Waves: Morphological and Mechanical Variation in *Mastocarpus papillatus* Along a Gradient of Force

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Abstract. Intertidal algae are exposed to the potentially severe drag forces generated by crashing waves, and several species of brown algae respond, in part, by varying the strength of their stipe material. In contrast, previous measurements have suggested that the material strength of red algae is constant across wave exposures. Here, we reexamine the responses to drag of the intertidal red alga *Mastocarpus papillatus* Kützting. By measuring individuals at multiple sites along a known force gradient, we discern responses overlooked by previous methods, which compared groups of individuals between “exposed” and “protected” sites. This improved resolution reveals that material strength and stipe cross-sectional area are both positively correlated with drag, suggesting that individual blades or populations can adjust either or both of these parameters in response to their mechanical environment. The combined effect of this variation is a stipe breaking force that is positively correlated with locally imposed drag. Owing to this response to drag, the estimated wave-imposed limit to thallus size in *M. papillatus* is larger than previously predicted and larger than sizes observed in the field, indicating that factors other than wave force alone constrain the size of this alga on wave-swept shores.

Introduction

Of all the organisms that inhabit the intertidal zone of rocky shores, sessile macroalgae face particularly great challenges in dealing with the effects of wave-induced water motion. Because algae lack the ability to “run and hide” during storms and their material strength is low rela-

tive to other biological materials (Denny *et al.*, 1989), algal distribution and abundance may be constrained by wave force (*e.g.*, Shaughnessy *et al.*, 1996). The question of whether algal populations respond to variation in wave intensity with morphological or mechanical adjustments to their shape or strength remains both open and intriguing.

Previous laboratory and field studies have demonstrated that some species of brown algae (Ochrophyta, class Phaeophyceae) exhibit considerable variability in breaking force, cross-sectional area, and material strength in response to differing exposure conditions (Charters *et al.*, 1969; Armstrong, 1987; McEacheron and Thomas, 1987; Gerard, 1987; Koehl and Alberte, 1988; Kraemer and Chapman, 1991a; Johnson and Koehl, 1994; Milligan and DeWreede, 2000). In contrast, no species of red algae (Rhodophyta) has revealed a correlation between mechanical properties and wave exposure, although differences in both biomass and planform area have been observed between exposed and protected sites (Carrington, 1990; Pratt and Johnson, 2002).

In this study, we assess the response of the common intertidal red alga *Mastocarpus papillatus* to varying levels of hydrodynamic force. In an attempt to uncover weak trends undetected in previous studies, we take a new approach to the measure of wave exposure. Whereas prior work has compared algal properties between groups of individuals from stretches of “exposed” and “protected” shore, we examine these same properties as they vary continuously along a measured gradient of imposed hydrodynamic force.

Drag is likely to be the most important hydrodynamic force applied to intertidal algae (Denny, 1988; Gaylord *et al.*, 1994), and as a result, it is the primary means by which algae interact mechanically with their flow environment. The force of drag, D , pulls an intertidal alga in the direction

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of water flow, and is a function of both water velocity and the shape and surface area of the alga:

$$D = \frac{1}{2}\rho U^2 S C_d \quad (1)$$

Here ρ is the density of seawater (nominally 1025 kg m^{-3}), U is water velocity (m s^{-1}), S is maximal planform area (m^2 , essentially half the wetted surface area of the frond), and C_d is the dimensionless coefficient of drag. In a comparison of groups of algae taken from "exposed" and "protected" sites, Carrington (1990) found no significant difference in stipe strength (breaking force divided by cross-sectional area at the breaking point) for *M. papillatus*, suggesting that the material properties of this species are not adjusted in response to its flow environment. However, this approach may be confounded by the fact that the planform area of this alga varies with wave exposure (Carrington, 1990). A small alga from a high-velocity, wave-exposed site might experience the same drag as a large alga from a lower-velocity, wave-protected site, in which case one might expect the strength of the two algae to be adjusted to similar values despite the difference in exposure. Here we explore how the morphological and mechanical properties of *M. papillatus* vary directly with imposed drag.

Materials and Methods

Species and location

Mastocarpus papillatus is perhaps the most common intertidal red alga along the central California coast (Abbott and Hollenberg, 1976); it grows in semi-erect clumps with multiple thalli emerging from a single crustose holdfast. ("Thallus" is the term for the combination of a stipe and the attached blade.) The alga's reproductive structures are contained in the papillae on the surface of each thallus, and, as a consequence, the potential reproductive output for a thallus is roughly proportional to its surface area (Bell, 1992). In this study, we take a single thallus as the sampling unit, without considering thallus location within a clump as a factor in the analysis. Although clumping reduces drag in the related alga *Chondrus crispus* (Johnson, 2001), Carrington (1990) found only mild drag-reducing interactions between groups of up to six closely packed thalli of *M. papillatus*. In this study, we did not encounter clumps larger than about a dozen densely packed individuals.

We collected samples from six sites along the rocky intertidal shore at Hopkins Marine Station (HMS), Pacific Grove, California ($36^\circ 37' \text{ N}$, $121^\circ 54' \text{ W}$). All sites were within 0.5 m of locations where dynamometers had previously been used to measure wave-induced forces as a function of offshore wave height (Helmuth and Denny, 2003). These measurements allowed us to choose, *a priori*, sites with a range of wave exposures. Although these sites were not spaced equally along the shore, they were roughly

equally spaced along a gradient of wave force. Sites were separated by a minimum of 10 m, and all were located at about 1.5 m above mean lower low water.

Data collection

We collected thalli during springtime low tides from April through June, 2003. Samples were fully hydrated before all experimental procedures to control for the possible effects of desiccation. We selected thalli that lacked obvious holes, tears, rotten areas, and other imperfections that could affect the breaking force. Thalli were selected with fewer than four major branches, as extensive branching patterns made accurate measurements of projected area difficult.

Blades were isolated from their neighbors and grasped with either a small alligator clip lined with rubber tubing or a small string tied with a slipknot. The clamp or string was attached to either a 500-g or a 1000-g recording spring scale (Pesola, resolution of $\sim 0.05 \text{ N}$) and pulled with a steady force intended to separate the blade from the substratum within about 1 second. A small slider on the scale recorded the force at which the thallus broke.

Only samples that broke just above the holdfast at the lower part of the stipe were included in subsequent analyses. We measured the diameter of the stipe at the breaking point for each sample with a dissecting microscope and ocular micrometer (resolution of $\sim 25 \mu\text{m}$), and estimated cross-sectional area at the breaking point as the area of a circle having this diameter. Stipe cross sections were very nearly circular, and we do not believe this approximation introduced substantial errors into our calculations. Each sample blade was then flattened under a sheet of clear acrylic and digitally photographed. The planform area of each sample was estimated using ImageJ, an image analysis program distributed by the Research Services Branch of the National Institutes of Health. We calculated the material strength of each blade by dividing the breaking force for that sample by the cross-sectional area over which the break occurred.

Drag calculations

We modeled the drag for each sample with the standard relationship given by Equation 1. The C_d used for this study was taken from Carrington (1990) and Bell (1999), who calculated the drag coefficient of *M. papillatus* as

$$C_d = 0.156 U^{-0.367}, U \leq 3.5 \text{ m s}^{-1} \quad (2)$$

$$C_d = 0.099, U > 3.5 \text{ m s}^{-1} \quad (3)$$

Thus,

$$D = 79.9 U^{1.633} S, U \leq 3.5 \text{ m s}^{-1} \quad (4)$$

$$D = 50.7 U^2 S, U > 3.5 \text{ m s}^{-1} \quad (5)$$

The appropriate units are subsumed into the leading numerical coefficient. Carrington (1990) noted that for velocities less than 3.5 m s^{-1} (the flow conditions at which drag measurements were conducted), this model of drag accounted for 75.8% of variation in drag for the 60 samples she examined. The addition of nine other morphological parameters, including patterns of branching and papillar density, explained only an additional 9% of the variation, and we did not include them in the model of drag for this study. Equations 2 and 3 take into account the reconfiguration (a decrease in projected area as a blade bends over) of *M. papillatus* in flow.

A bottom-mounted wave gauge (SeaBird SBE26) deployed offshore at HMS measured significant wave height (the height of the highest one-third of waves) four times per day for 40 days just before the beginning of this study. We used the average significant wave height during this period (1.3 m) to calculate the relevant maximal water velocity for each site from the relationships reported by Helmuth and Denny (2003). These velocity calculations provide an estimate of the typical daily maximum velocity experienced by *M. papillatus* thalli at each sampling site over the 40 days immediately prior to the beginning of this study. Using this velocity and Eq. 1, we calculated the typical maximum drag imposed on each individual and used this as an index of the maximum force to which the individual thallus is subjected.

Statistical analyses were conducted using Systat 8.0 (SPSS Inc., Chicago, Illinois).

Results

We sampled a total of 121 fronds. All data (cross-sectional area, breaking force, material strength, drag) were \log_{10} -transformed prior to regression to correct departures from normality.

The results of our three ordinary-least-squares regressions are reported in Table 1. There are positive relationships between breaking force and drag (Fig. 1A, $r^2 = 0.212$, $P < 0.001$), cross-sectional area and drag (Fig. 1B, $r^2 =$

Table 1

Breaking force, stipe cross-sectional area, and stipe strength all increase with an increase in drag: results from regressions on \log_{10} - \log_{10} transformed data

Regression	Intercept	Slope	P	r^2
Breaking force on Drag	0.683	0.316	< 0.001	0.212
Cross-sectional area on Drag	-6.171	0.154	0.009	0.048
Strength on Drag	0.854	0.162	0.007	0.053

Probability values reported are the outcome of two-tailed Student's *t* tests against the null hypothesis that the slope estimates equal zero: $n = 121$ in all cases.

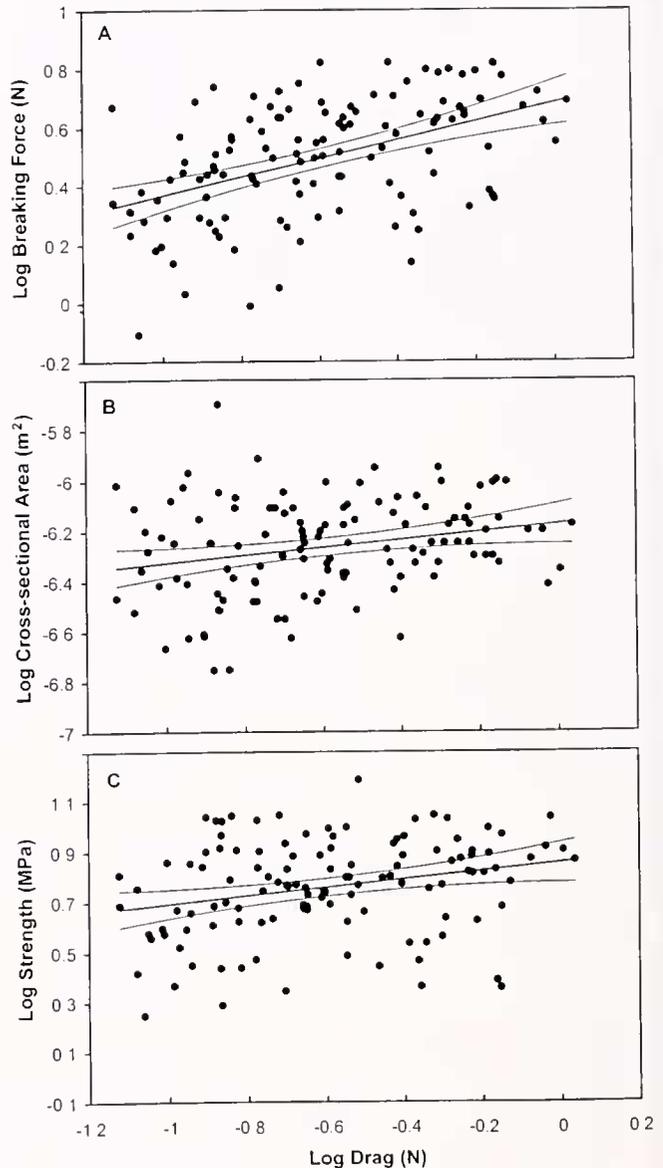


Figure 1. The \log_{10} of (A) measured breaking force, (B) stipe cross-sectional area, and (C) material strength as a function of the \log_{10} of calculated average maximal drag. Outer lines represent 95% confidence intervals on the regression. ($n = 121$; A: $r^2 = 0.212$, $P < 0.001$; B: $r^2 = 0.048$, $P = 0.009$; C: $r^2 = 0.053$, $P = 0.007$)

0.048, $P = 0.009$), and material strength and drag (Fig. 1C, $r^2 = 0.053$, $P = 0.007$); all are significant at the $\alpha = 0.017$ level ($\alpha = 0.05$ with a Dunn-Šidák correction for multiple comparisons).

Discussion

Relationships along a drag gradient

Breaking force for *Mastocarpus papillatus* increases with increasing drag (Fig. 1A), implying that these algae respond

to their wave environment. This increase in breaking force can be due to an increase in stipe cross-sectional area, an increase in the breaking strength of the stipe material, or both. The trends shown in Figure 1B and 1C suggest that both adjustments are present in *M. papillatus*. The correlations between drag and strength, cross-sectional area, and breaking force may be the result either of selective forces acting on the population as a whole (by removing weak individuals) or of plastic responses to increased drag forces within individual thalli. Further investigation is needed to determine which of these two effects occurs in *M. papillatus*.

Our observed increases in stipe breaking force, cross-sectional area, and material strength with increasing drag stand in contrast to previously published results. Pratt and Johnson (2002) found no significant relationships between any of these three variables and wave exposure for the related algae *Mastocarpus stellatus* and *Chondrus crispus* when they compared groups of algae between exposed and protected sites. Carrington *et al.* (2001) also found no variation in tissue strength in *C. crispus* when using an exposed-versus-protected experimental design. Examining both *M. stellatus* and *C. crispus*, Dudgeon and Johnson (1992) report evidence that high wave exposure and freezing actually lower the strength of the stipes in these algae. Working with *M. papillatus*, Carrington (1990) found no significant differences in stipe strength among samples collected from sites characterized as exposed, protected, and intermediate-exposure.

The relationships between cross-sectional area and drag, although statistically significant, explains only 4.8% of the overall measured variability in cross-sectional area. Similarly, the relationship between strength and drag accounts for only 5.3% of the overall variation in strength. Thus, the natural variation within this *M. papillatus* population is large compared to the magnitude of the predictable adjustment of either cross-sectional area or strength with increasing drag. Given this variability, it is not surprising that studies based on a categorical comparison (exposed versus protected) failed to discern a relationship. Sampling techniques that directly quantify the drag on each individual, and therefore allow for calculation of the correlation between drag and morphological and mechanical parameters, are needed to detect such relatively weak signals. A tech-

nique similar to that used here has been used to measure the plastic variation in length of barnacle feeding legs as a function of flow speed (Arsenault *et al.*, 2001; Li and Denny, 2004).

Despite these high levels of natural variation, the observed increases in cross-sectional area and strength across the force gradient at Hopkins Marine Station may be biologically significant, an effect that may be obscured by the logarithmic plots shown in Figure 1. On average, cross-sectional area varies by 20%–25% and strength by 25%–30% over the range of drag sampled in this study, and together these trends contribute to a twofold variation in breaking force. Thus, despite the high degree of variability in these graphs and the lack of predictive power they imply, differences in strength and cross-sectional area across a drag gradient may still be of biological importance for individuals of this species.

The biological mechanisms by which tissue strength varies in red algae are unknown, although previous studies on brown algae suggest that the types and amounts of structural materials, the proportions of these materials, and the orientation of fibers in thalli may play a role (Wainwright *et al.*, 1976; Koehl and Wainwright, 1977; Babb, 1985). Modification of cell wall composition, including an augmentation of structural compounds, in response to wave forces has also been previously documented for brown algae (Kraemer and Chapman, 1991a). Kraemer and Chapman (1991b) also noted an increase in the incorporation of radioactively tagged carbon into cell wall tissue of *Egregia menziesii* under the application of a continuous force, which may play a role in strength variation.

Comparison with data from Carrington (1990)

Many of the results of this study corroborate the previous work of Carrington (1990), also at Hopkins Marine Station; a brief comparison is given in Table 2. The difference in the percentage of holdfast failures might be explained by seasonal differences: our study was conducted in spring and Carrington's in winter. Variation in the properties of *M. papillatus* between seasons has yet to be examined. Carrington reports a slightly larger mean cross-sectional area than we measured (Student's *t* test with unequal variances, $P = 0.005$). Since we find that cross-sectional area varies

Table 2

Comparison with data from Carrington (1990): although stipe strength is similar between these studies, our thalli had slightly smaller stipe cross sections and a higher incidence of holdfast failures

Calculations	Carrington (1990)	This study
Holdfast failures (%)	12% ($n = 83$)	36% ($n = 240$)
Mean stipe strength	6.73 MN/m ² ($n = 73$, SD = 2.83)	6.27 MN/m ² ($n = 121$, SD = 0.233)
Mean stipe cross-sectional area	0.71 mm ² ($n = 125$, SD = 0.34)	0.60 mm ² ($n = 121$, SD = 0.27)

with wave environment, this difference may be due to a higher average drag for Carrington's samples. Carrington's study did not include drag values, however, so this hypothesis cannot be tested. There is no significant difference between the two means of stipe strength (Student's t test with unequal variances, $P > 0.10$). Carrington found no differences among the mean stipe strength for her exposed, intermediate, and protected sites. However, our results suggest that within each of her sites she may have sampled across a variety of microhabitats, obscuring the relationships we found. Additional variation between our results and Carrington's could also be explained by the greater resolution of our measurements: we measured breaking force to the nearest 0.05 N and cross-sectional diameter to the nearest 25 μm ; Carrington measured these two quantities to the nearest 1 N and 50 μm , respectively.

Predictions of maximum attainable size

Carrington found no significant relationship between cross-sectional area of the stipe and thallus planform area ($P \gg 0.05$), and neither did we ($r^2 = 0.023$, $P = 0.054$). Operating under the assumption that equal stipe cross-sectional area implied equal breaking force across blade sizes, Denny and Wethey (2001) proposed that Carrington's data could be used to predict the maximum size a blade could attain at a given water velocity. Setting Equation 4 (the expression for measured drag at low velocities) equal to the mean breaking force of Carrington's sample (4.8 N) and solving for planform area, they obtained the relationship:

$$S_{\max} = 0.060 U^{-1.633} \quad (6)$$

Maximum blade area (and, therefore, maximum potential reproductive output) are predicted to decrease rapidly with increasing water velocity (Fig. 2).

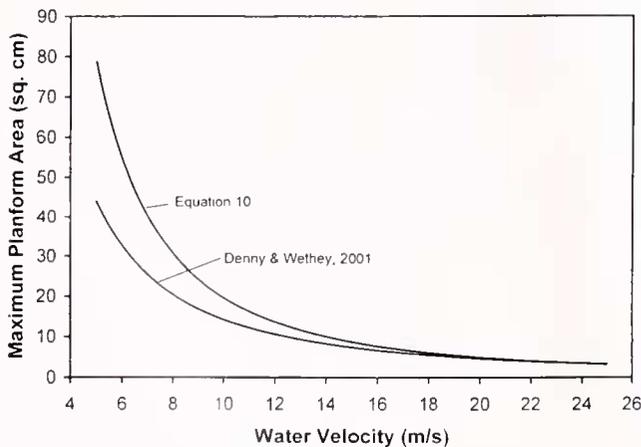


Figure 2. Prediction of maximum attainable frond size according to equation 10 ($S_{\max} = 0.095 U^{-2}$) and Denny and Wethey (2001, $S_{\max} = 0.060 U^{-1.633}$).

This prediction should be modified in two respects, however. First, Denny and Wethey (2001) assumed that the drag coefficient decreases steadily as velocity increases (Equation 2), but Bell (1999) suggests that the drag coefficient at the high velocities is constant (Equation 3). As a result, Equation 5 rather than Equation 4 should be used to describe the drag force imposed on a thallus. Second, in contrast to the supposition of Denny and Wethey (2001), our results (Table 1, Fig. 1A) show that breaking force, F , is not constant. On average:

$$\log(F) = 0.683 + 0.316 \log(D) \quad (7)$$

$$F = 4.820 D^{0.316} \quad (8)$$

Inserting Equation 5 (the appropriate expression for drag) into Equation 8 (the expression for breaking force), we obtain an equation for breaking force as a function of water velocity and thallus area:

$$F = 16.67 U^{0.632} S^{0.316} \quad (9)$$

Equating this expression for breaking force with Equation 5 (the expression for drag at high velocities) and solving for planform area, we find that

$$S_{\max} = 0.198 U^{-2} \quad (10)$$

This relationship is also shown in Figure 2. At low velocities, the maximum sizes it predicts are substantially larger than those predicted by Denny and Wethey (2001), and the two curves cross at a velocity of approximately 20 m s^{-1} .

The predictions of both Equations 6 and 10 appear to be larger than the sizes observed in nature. For example, *M. papillatus* is virtually absent at sites along the shore at Hopkins Marine Station that are exposed to average maximum water velocities in excess of 10 m s^{-1} , despite the prediction of Denny and Wethey (2001) that a relatively large blade of 14 cm^2 (or our prediction that an even larger blade of 20 cm^2) could survive that velocity. This disparity could have at least two causes. First, sites with an average maximum water velocity of 10 m s^{-1} may occasionally be exposed to much higher velocities (Helmuth and Denny, 2003), and it may be these rare high velocities (rather than the average maximum velocity) that limit the size and distribution of *M. papillatus*. For example, by either prediction, the single imposition of a water velocity of 20 m s^{-1} would remove all blades larger than 5 cm^2 . Second, wave forces may not be the only constraint on the size of *M. papillatus* on wave-swept shores. Samples that exhibited weakening of the stipe tissue due to storm damage, repeated stress, grazing, or other factors were not included in our collection for this study. It seems likely that biotic and nonhydrodynamic abiotic stressors such as these reduce the maximum size (and reproductive output) attainable by a

frond in the field to below the size we have estimated here for intact fronds.

Conclusions

When examined along a continuous gradient of wave force, *Mastocarpus papillatus* exhibits statistically significant increases in breaking force, cross-sectional area, and material strength with an increase in estimated drag, although there is substantial variation about this trend. The finer resolution of this microhabitat-based approach allows us for the first time to discern these trends in an alga of the order Rhodophyta.

Attention should be paid to the possible biological explanations behind these relationships, especially to the relationship between strength and drag. Possible chemical or physical variation within *M. papillatus* tissue itself, particularly in the cell wall composition, might help explain this relationship.

Predictions of the wave-limited size of this alga indicate that factors other than simply wave force contribute to limiting the size of fronds in the field.

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Literature Cited

- Abbott, J. A., and G. J. Hollenberg. 1976. *Marine Algae of California*. Stanford University Press, Stanford, CA. 827 pp.
- Armstrong, S. L. 1987. Mechanical properties of the tissues of the brown alga *Hedophyllum sessile* (C. Ag.) Setchell: variability with habitat. *J. Exp. Mar. Biol. Ecol.* **114**: 143–151.
- Arsenault, D. K., K. B. Marchinko, and A. R. Palmer. 2001. Precise tuning of barnacle leg length to coastal wave action. *Proc. R. Soc. Lond. B* **268**: 2149–2154.
- Babb, I. 1985. The biomechanics of Maine coast kelps: their distribution, morphology, and mechanical properties. M.Sc. thesis, University of Maine, Orono. 126 pp.
- Bell, E. C. 1992. Consequences of morphological variation in an intertidal macroalga: physical constraints on growth and survival of *Mastocarpus papillatus* Kützting. PhD. thesis, Stanford University.
- Bell, E. C. 1999. Applying flow tank measurements to the surf zone: predicting dislodgment in the Gigartinales. *Phycol. Res.* **47**: 159–166.
- Carrington, E. 1990. Drag and dislodgment of an intertidal macroalga: consequences of morphological variation in *Mastocarpus papillatus* Kützting. *J. Exp. Mar. Biol. Ecol.* **139**: 185–200.
- Carrington, E., S. P. Grace, and T. Chopin. 2001. Life history phases and the biomechanical properties of the red alga *Chondrus crispus* (Rhodophyta). *J. Phycol.* **37**: 699–704.
- Charters, A. C., M. Neushul, and C. Barilotti. 1969. The functional morphology of *Eisenia arborea*. *Proc. Int. Seaweed Symp.* **6**: 89–105.
- Denny, M. W. 1988. *Biology and the Mechanics of the Wave-Swept Environment*. Princeton University Press, Princeton, NJ.
- Denny, M., and D. Wethey. 2001. Physical processes that generate patterns in marine communities. Pp. 3–37 in *Marine Community Ecology*, M. Bertness, S. Gaines, and M. Hay, eds. Sinauer Associates, Sunderland, MA.
- Denny, M. W., V. Brown, E. Carrington, G. Kraemer, and A. Miller. 1989. Fracture mechanics and the survival of wave-swept macroalgae. *J. Exp. Mar. Biol. Ecol.* **127**: 211–228.
- Dudgeon, S. R., and A. S. Johnson. 1992. Thick vs. thin: thallus morphology and tissue mechanics influence differential drag and dislodgment of two co-dominant seaweeds. *J. Exp. Mar. Biol. Ecol.* **165**: 23–43.
- Gaylord, B., C. A. Blanchette, and M. W. Denny. 1994. Mechanical consequences of size in wave-swept algae. *Ecol. Monogr.* **64**: 287–313.
- Gerard, V. A. 1987. Hydrodynamic streamlining of *Laminaria saccharina* Lamour in response to mechanical stress. *J. Exp. Mar. Biol. Ecol.* **107**: 237–244.
- Helmuth, B., and M. W. Denny. 2003. Predicting wave exposure in the rocky intertidal zone: do bigger waves always lead to larger forces?. *Limnol. Oceanogr.* **48**: 1338–1345.
- Johnson, A. S. 2001. Drag, drafting, and mechanical interactions in canopies of the red alga *Chondrus crispus*. *Biol. Bull.* **201**: 126–135.
- Johnson, A. S., and M. A. R. Koehl. 1994. Maintenance of dynamic strain similarity and environmental stress factor in different flow habitats: thallus allometry and material properties of a giant kelp. *J. Exp. Mar. Biol. Ecol.* **195**: 381–410.
- Koehl, M. A. R., and R. S. Alberte. 1988. Flow, flapping, and photosynthesis of *Nereocystis leutkeana*: a functional comparison of undulate and flat blade morphologies. *Mar. Biol.* **99**: 435–444.
- Koehl, M. A. R., and S. A. Wainwright. 1977. Mechanical adaptations of a giant kelp. *Limnol. Oceanogr.* **22**: 1067–1071.
- Kraemer, G. P., and D. J. Chapman. 1991a. Biomechanics and alginic acid composition during hydrodynamic adaptation by *Egregia menziesii* (Phaeophyta) juveniles. *J. Phycol.* **27**: 47–53.
- Kraemer, G. P., and D. J. Chapman. 1991b. Effects of tensile force and nutrient availability on carbon uptake and cell wall synthesis in blades of juvenile *Egregia menziesii* (Turn.) Aresch. (Phaeophyta). *J. Exp. Mar. Biol. Ecol.* **149**: 267–277.
- Li, N. K., and M. W. Denny. 2004. Limits to phenotypic plasticity: flow effects on barnacle feeding appendages. *Biol. Bull.* **206**: 121–124.
- McEacheron, J. C. T., and M. L. H. Thomas. 1987. Attachment strength of *Ascophyllum nodosum* (L.) LeJolis and exposure to wave action. *Bot. Mar.* **30**: 217–222.
- Milligan, K. L. D., and R. E. DeWreede. 2000. Variations in holdfast attachment mechanics with development stage, substratum-type, season, and wave exposure for the intertidal kelp species *Hedophyllum sessile* (C. Agardh) Setchell. *J. Exp. Mar. Biol. Ecol.* **254**: 189–209.
- Pratt, M. P., and A. S. Johnson. 2002. Strength, drag, and dislodgment of two competing intertidal algae from two wave exposures and four seasons. *J. Exp. Mar. Biol. Ecol.* **272**: 71–101.
- Shaughnessy, F. J., R. E. DeWreede, and E. C. Bell. 1996. Consequences of morphology and tissue strength to blade survivorship of two closely related Rhodophyta species. *Mar. Ecol. Prog. Ser.* **136**: 257–266.
- Wainwright, S. A., W. D. Biggs, J. D. Currey, and J. M. Gosline. 1976. *Mechanical Design in Organisms*. Edward Arnold, London. 423 pp.